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Short report

Bottlenose dolphins do not behave prosocially in an instrumental helping task

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ABSTRACT

Although bottlenose dolphins (*Tursiops truncatus*) are known for being a highly social species that live in complex societies that rely on coalition formation and cooperative behaviours, experimental studies on prosocial behaviour in this species are scarce. Helping others reach their goals (instrumental helping) is considered as an example of prosocial behaviour. Thus, in this pilot study, we examined whether a group of five captive bottlenose dolphins would behave prosocially in an instrumental helping task. Dolphins were given the opportunity to share tokens that allow their partners to obtain a preferred toy. Dolphins were tested in their free time and they could choose to share the tokens or do nothing. None of the dolphins shared the tokens, instead, they preferred to play with them, ignoring their partners. They did transfer the tokens to other sides of the pool but out of the reach of their partners. Therefore, this group of dolphins did not spontaneously help their partners in this task, showing no preference for other-regarding behaviour in this context.

1. Introduction

Other-regarding preferences refer to whether an individual is sensitive to another's payoffs indicating, thus, the presence of a prosocial predisposition to benefit others (Yamamoto and Tanaka, 2010). Helping others at a very low or no cost to oneself is an example of this capacity. Helping behaviour is considered to be an example of prosocial behaviour (Batson and Powell, 2003), which promotes the well-being of another individual with no immediate benefit to oneself. This helping behaviour is costly and evolutionarily rare when directed toward non-kin (Warneken and Tomasello, 2006).

There are just a few experimental studies on helping behaviour in non-human species. Partly because it is unethical to create situations in which animals experience intense emotions such as distress or pain to test their conspecific's responses. Thus, it is a difficult task to experimentally assess animals' helping responses towards distressed conspecifics. Therefore, most of the available experimental studies on helping behaviour in non-human animals are focused on instrumental helping and other-regarding preferences. These paradigms seem to be a good alternative to examine some of the factors and situations that favour helping responses in animals because they do not require eliciting distress in the experimental subjects. Instrumental helping is a behaviour performed by an individual that enables another to reach a goal that cannot be achieved otherwise (Greenberg et al., 2010; Melis, 2017). It requires a cognitive evaluation of the other's situation and seems also to involve other-regarding preferences (de Waal, 2008; Yamamoto et al., 2012). Importantly, instrumental helping paradigms allow varying motivational factors, such as the identity of the recipient or the cost of the helping responses, as well as cognitive factors, like the difficulty of the instrumental context (Skerry et al., 2011). Motivational and cognitive variables have proven to be the main factors influencing animals' prosocial responses (Skerry et al., 2011).

Research on other-regarding preferences in non-human animals has failed to provide clear-cut results. In this field, tasks assessing whether animal species display a tendency to give food to others have been widely used and the obtained results varied across species and paradigms. For example, whereas in some studies several primate species did not show other-regarding preferences (Amici et al., 2014; Burkart and van Schaik, 2013; Cronin et al., 2009; Drayton and Santos, 2014; Jensen et al., 2006; Kim et al., 2015; Silk et al., 2005; Stevens, 2010; Vonk et al., 2008), in other studies the same or related species provide or share food with others (Brosnan et al., 2010; Burkart et al., 2007; Burkart and van Schaik, 2013; Claidière et al., 2015; de Waal et al., 2008; Lakshminarayanan and Santos, 2008; Takimoto et al., 2010; Tan and Hare, 2013). Therefore, it has been suggested that specific traits related to a species' social organization could also be an important factor related to other-regarding preferences (Dale et al., 2019). In turn, studies on instrumental helping in chimpanzees (*Pan troglodytes*)

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showed that these animals provide flexible targeted helping according to another individual's situation (e.g. transferring a tool to a partner) (Yamamoto et al., 2012, 2009). But, although they seemed to understand their partner's need, chimpanzees rarely helped proactively (Yamamoto, 2017). That is, chimpanzees provided helping responses only upon a partner's request (Yamamoto et al., 2009). Conversely, capuchin monkeys (*Cebus apella*) did not exhibit strong prosocial preferences in instrumental helping tasks. These monkeys failed to take into account the perspective of others when they expected to get food for themselves (Barnes et al., 2008). They also failed to help a conspecific in a minimal-cost instrumental helping task, not sharing tokens that allow the other monkey to obtain food from an apparatus ("vending machine") (Skerry et al., 2011).

In general, studies on instrumental helping in species other than primates are scarce and further research is needed. Bottlenose dolphins (*Tursiops truncatus*) are excellent candidates for this endeavour as they are a highly social species endowed with sophisticated cognitive abilities (Herman, 2010; Pack and Herman, 2006). In the wild, bottlenose dolphins perform diverse prosocial behaviours such as epimeletic care and rescue behaviour (Caldwell and Caldwell, 1966; Cockcroft, 1990; Kuczaj et al., 2001; Siebenaler and Caldwell, 1956). Furthermore, they also engage in several cooperative activities (Eskelinen et al., 2016; Jaakkola et al., 2018; King et al., 2016; Kuczaj et al., 2015). A recent study (Nakahara et al., 2017) examined whether bottlenose dolphins behave prosocially in two different paradigms involving enrichment items (showers) instead of food rewards. The first experiment was a prosocial choice task in which the subject could choose between two options: (1) both individuals take a shower, or (2) only the subject receives the reward. In the second experiment, the subject could either instrumentally help its partner to take a shower or do nothing. In the prosocial choice task, dolphins significantly chose the prosocial option without partner's request. Conversely, dolphins did not help their partner in the giving assistance task. Therefore, it remains to be further clarified the extent to which bottlenose dolphins show other-regarding preferences and provide instrumental helping to others.

Thus, in this pilot study, we examined whether captive bottlenose dolphins would spontaneously behave prosocially in an instrumental helping task adapting to dolphins the protocol used by Skerry et al. (2011) with capuchin monkeys.

2. Materials and methods

2.1. Subjects and housing

Five Atlantic bottlenose dolphins (*T. truncatus*) housed at Marineland Mallorca participated in this study: three males *Blue*, *Mateo*, *Aitamy* (25, 13 and 7 years old), and two females *Blava* and *Stella* (13 and 8 years old). All the dolphins were captive born. The dolphins lived in a social group in an outdoor main pool (324.43 m^2 surface area, 5 m deep) conjoined to two small pools (18.91 m^2 surface area, 2 m deep / 127.37 m^2 surface area, 5 m deep) with a total volume of 2296.82 m^3 of water. The experiment was conducted during their free time before the first training session of the day, without any food reinforcement. The dolphins were never deprived of food in any way. The subjects participated in the study voluntarily. The park was closed to the public for the duration of the experiment.

2.2. Apparatus

Fig. 1 shows the basic apparatus and testing setup. In this study, several plastic hoops (20 cm diameter) served as tokens that could be exchanged for dolphins' preferred toy, a rubber ball (70 cm circumference). In this park, balls were often used by the trainers as rewards during the training sessions. Balls were stored in a transparent plastic box near the pool for the dolphins to have visual access to them. The main pool could be separated from the other two pools by two vertical sliding gates made of canvas or mesh and mounted on a stainless-steel frame that made it impossible for dolphins to pass from one pool to the other. All sessions were videotaped using three waterproof cameras SJCAM SJ4000 located in three different areas of the enclosure.

2.3. Design and procedure

2.3.1. Training

During the training sessions, the gates were open and dolphins had free access to all the pools. Dolphins were trained in their free time to exchange tokens (hoops) for their preferred toy (ball) with an experimenter. At the beginning of each training session, the experimenter threw the tokens to the pool and waited until a dolphin approached with a hoop. The experimenter sometimes pointed to a token to motivate the dolphins to pick the hoop and give it to her. At the end of the training phase, the procedure was standardized. First, the experimenter carrying both the tokens and the balls approached the edge of the main pool. Then, she threw the tokens into the main pool (one per individual) and she moved with the box to the medical pool. She placed the box out of dolphins' reach but still visible from the dolphins' perspective. The dolphins had to collect a token from the main pool, take it to the medical pool where the experimenter was and give the hoop to her to get the ball. The experimenter never exchanged balls for tokens in the main pool. When all dolphins showed evidence of success with this procedure by exchanging the tokens with the trainer on at least three separate days, we passed to the testing phase.

2.3.2. Testing

The testing sessions were conducted during dolphins' free time, before the first training session of the day. During the testing sessions two gates were closed and the main pool was separated from the other two pools. Dolphins were divided into two groups: the helper group and the recipient group. The helper group stayed in the main pool and had access to the tokens but could not exchange them with the experimenter. Conversely, the recipient group stayed in the small pools and had the opportunity to interact with the experimenter but no access to the tokens.

Composition and the distribution of the group were left to the trainers' decision to cause the minimum stress possible to the animals. Before each experimental session, the trainers divided the dolphins into two groups closing the sliding gates and rewarding the dolphins with fish at the end of the procedure. The juvenile male had previously refused to be alone with the two adult males so only six of the seven possible combinations of interacting individuals could be tested.

Dolphins were tested in the same three experimental conditions as the capuchin monkeys in Skerry et al.'s (2011) study:

2.3.2.1. Goal condition. The helper group received the tokens (3 per individual) but could not exchange them with the experimenter, whereas the recipient group could interact with the experimenter but had no access to the tokens. The helper group had the opportunity to help the recipients by passing the tokens above the gate or throwing them over the wall of the main pool (Fig. 1b), as they used to do with other toys in their free time.

2.3.2.2. No-goal condition (control 1). This condition was identical to the goal condition except that the experimenter and the balls were absent. Thus, the recipients did not have the opportunity to interact with the experimenter. The aim of this control condition was to rule out the possibility that the dolphins transferred tokens simply because they preferred to pass tokens over walls or passing toys to a conspecific.

2.3.2.3. No-recipient condition (control 2). The experimenter and the balls were present, but all the dolphins remained in the main pool with the tokens. Thus, there were no recipients to exchange tokens with the

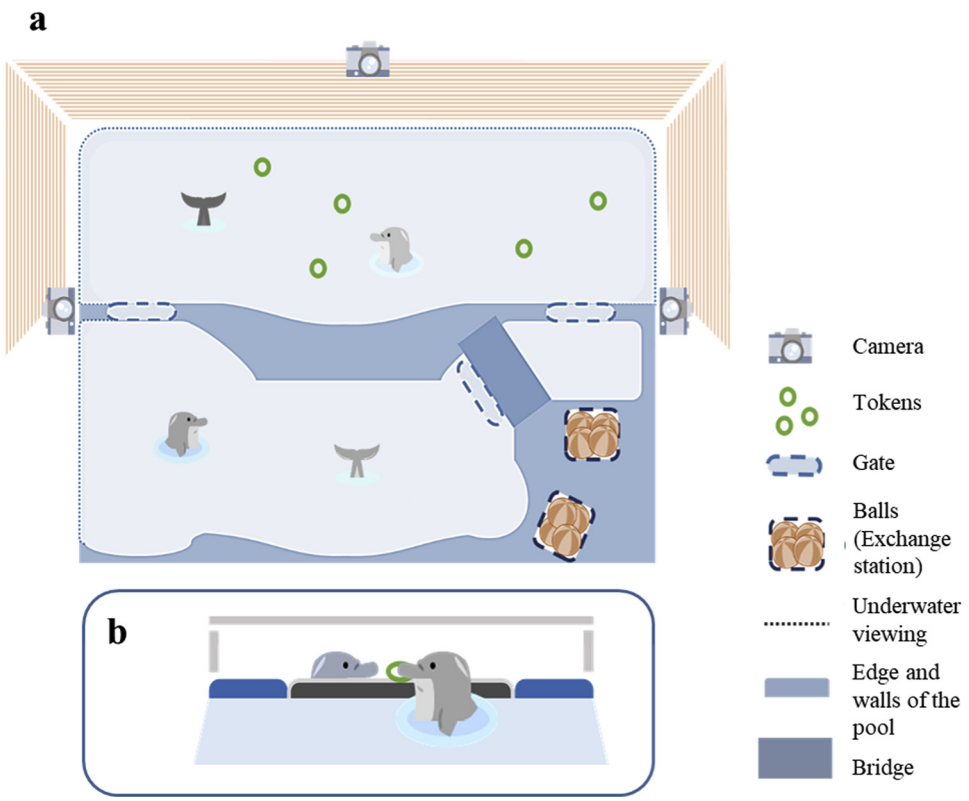

Fig. 1. a. Facility, basic apparatus, testing-up and camera placement in this study. **b.** View of a closed gate during the experimental sessions.

experimenter. The aim of this control condition was to rule out the possibility that the presence of the experimenter with the balls elicited somehow the token transfer.

The frequency of token transfer in the goal condition was compared to the frequency of transfers in the two control conditions. The frequency of token transfer to other sides of the pool was also recorded. Dolphins received 13 experimental sessions: six sessions of the goal and no-goal conditions (10 min per session) and one session (10 min) of the no-recipient condition. Each dolphin received at least two sessions in the role of the helper and two sessions in the role of the recipient in the goal and no-goal conditions. In four of these sessions, the helper group was comprised of three individuals and two in the remaining sessions. Testing sessions were divided into blocks of 2 sessions per day (one session of the goal condition followed by one session of the no-goal condition). On the last day of testing, they only received one session of the no-recipient condition. Dolphins were tested on two consecutive days per week for a total of seven days. In the day following the two consecutive testing days, they received a reminder training session to avoid frustration (three reminder training sessions, one per week). This testing schedule was adapted to meet the time constraints imposed by the park. As the separation of the dolphins in groups required a considerable time and the participation of several trainers, we decided to test the dolphins in two experimental conditions per day, goal and no-goal conditions, using the same group distribution in both conditions. Therefore, we left the no-recipient condition, which required another group distribution, for the end of testing. We decided not to counterbalance the order of the goal and no-goal conditions since the dolphins could learn that after the no-goal condition it always follows the goal-condition. In that case, it was possible that in the no-goal condition the dolphins also transferred the tokens to help their partners, and thus this condition wouldn't be an appropriated control test.

3. Results

Four dolphins attained the testing criterion after six training sessions. We decided to move to the testing phase even though *Blue* did not attain the testing criteria since his failure was likely related to being blind in the right eye.

None of the dolphins shared the tokens in the goal condition or in the no-recipient condition. Only one dolphin transferred one of the tokens in one session of the no-goal condition (Mean transfers $\pm$ SE = 0.17 $\pm$ 0.16). Furthermore, we did not observe any clear attempt to pass the tokens. Although during the experimental sessions, dolphins did not pass the tokens to their partners, some dolphins did transfer the hoops to other sides of the enclosure. Specifically, they threw the tokens above the glass walls of the tank (Mean transfers $\pm$ SE = 0.83 $\pm$ 0.47). These walls were located on the opposite side of the pools of the receiver group (see Fig. 1a). Finally, both females exchanged tokens for balls in the three reminder training sessions, whereas *Aitamy* did so in two sessions and *Mateo* in one.

4. Discussion

In this task, dolphins did not spontaneously share tokens with other conspecifics. Our results are consistent with those of the study of Nakahara et al. (2017). Importantly, dolphins did not differentiate between conditions, not transferring tokens in any of the conditions tested, independently of whether the experimenter was present or not, and irrespectively of whether there was a recipient in the other pool or not. Only one dolphin transferred one token in the no-goal condition.

Several methodological problems have been proposed as the main factors behind failure in tasks assessing prosocial and cooperative behaviours in non-human animals (Albiach-Serrano, 2015). These methodological problems are related to both social and physical elements of the tasks (Albiach-Serrano, 2015; Skerry et al., 2011). Thus, it is possible that, in this experiment, the lack of helping responses of dolphins could be related to some of these aspects of the study design. Furthermore, the limitations of testing in captive settings could constrain the interpretation of the results with regard to the subjects' underlying abilities (Marino and Frohoff, 2011).

The identity of the recipient could influence the subjects' motivation to help. In fact, prosocial behaviours seem to follow a familiarity gradient (Preston and de Waal, 2002). In this experiment, dolphins could provide help to several familiar conspecifics thus, they were expected to be motivated to behave prosocially towards them. However, dolphins did not pass any token to the recipient group. The cost of helping and the presence of motivating rewards are other motivational factors that could have affected dolphins' behaviour in the task. During the training, though, most of the dolphins were highly motivated to obtain balls for themselves, exchanging tokens almost immediately after the start of the session. Sometimes, when they lost the ball they immediately searched for a token and exchanged it to obtain a new one, suggesting that they understood the dynamics of the token exchange. We also observed that during the experimental sessions the recipient dolphins attempted to get the experimenter's attention and tried to get the balls in several ways. Thus, it seems that the balls were indeed a valuable object for this group of dolphins. To minimize the cost associated with sharing the tokens, dolphins were given many of them. So, even if they shared a token with a partner they still had some left with which to play. Furthermore, the action of transferring a token to the other pools did not seem to require a great amount of effort (Fig. 1b). In fact, during the test, some of the dolphins played with the tokens by throwing them in the air and over the glass tank walls to other sides of the enclosure, out of their partners' reach. It is also possible that the dolphins did not share tokens because they were motivated to obtain later the reward for themselves. However, dolphins were tested in several experimental sessions, so they had the opportunity to learn that, even though they kept the tokens, they could not exchange them with the experimenter. In any case, to control for this constraint, it would be interesting to retest dolphins using a non-mobile exchange machine similar to that used in Skerry et al.'s paradigm, in which dolphins can deposit a token and obtain a reward.

Providing prosocial responses in instrumental tasks may depend on the ability of the subject to infer another's goals and the salience and ease with which the subject can infer this goal from the situation (Skerry et al., 2011; Vonk et al., 2008). For example, chimpanzees seemed to behave prosocially in tasks where goals are made salient or as long as the partner requested help (Melis et al., 2011; Warneken et al., 2007; Warneken and Tomasello, 2006; Yamamoto et al., 2009). Conversely, in a prosocial choice task, dolphins chose the prosocial option spontaneously, without requests from the partner (Nakahara et al., 2017). In our experiment, subjects were familiar with the specific goal of the recipients not only because they have been previously trained to exchange tokens for rewards but also because the roles were reversed across sessions. Despite the simplicity of the task, it could be possible that the dolphins were unable to attribute or infer the recipients' goal or to integrate relevant representations to successfully help their partners. Although it has been shown that dolphins are endowed with well-developed cognitive skills (Pack and Herman, 2006; Xitco et al., 2004, 2001), to date there is no positive evidence of goal attribution in dolphins.

This experiment was conceived as an initial attempt to assess spontaneous helping responses in captive dolphins, thus we kept the task as simple as possible, not training the dolphins to transfer the tokens from one pool to another, and not reinforcing them for doing so. These dolphins used to play passing toys from one pool to another, so it was therefore plausible that dolphins spontaneously used this knowledge for devising a way to transfer the tokens during the test. However, we cannot rule out the possibility that the lack of prosocial responses was due to dolphins' inability to find a way to transfer the tokens rather than due to a lack of prosocial preferences. On the other hand, the fact that we did not observe any clear attempt to pass the tokens suggest that dolphins did not even try to help their partners. Furthermore, we observed that, after giving the tokens to the helper group, dolphins picked up one and approached and looked over the gate located in front of the experimenter. When dolphins saw that they could not pass to the other side they swam away from the gate. Thus, the dolphins could have realized that the tokens were inaccessible and lost interest in the situation. Therefore, apart from the social and physical constraints of the task, another explanatory alternative might be that dolphins were indifferent to the opportunity to help others in this context. This result should not be surprising given that sharing toys or other resources is difficult even for human young children (Brownell et al., 2013). In order to assess whether the difficulty of the task lies in innovation, it would be of great interest to give the dolphins enough experience passing tokens through the gates and retest them in a subsequent study. For example, one possibility is to first train one individual to solve the task and then observe whether this manipulation prompts the adoption of prosocial behaviours in the group. Future studies could also include in the familiarization phase a human demonstrator in both the helper and recipient role. This condition would allow the opportunity for social learning but without reinforcement.

By adapting the instrumental helping task used by Skerry et al. (2011) with capuchins, we were able to test the dolphins in groups. This type of setup has not been extensively used in experimental studies assessing prosocial behaviours or other-regarding preferences in animals. Testing animals in groups allows for the opportunity of social learning, a factor that seems to be crucial for the dissemination of certain behaviours in animals (e.g. Vale et al., 2017). Furthermore, we designed this protocol in a way that it also served to examine possible cooperative or reciprocal responses across sessions: the number of tokens and balls was in excess to allow for the possibility that the individuals in the receiver group could keep exchanging the tokens received from the helper group so that the balls could be obtained for all members of the group.

Dolphins have been reported to perform several prosocial behaviours such as rescuing or caring for other individuals in the wild and in captivity (Caldwell and Caldwell, 1966; Cockcroft, 1990; Kuczaj et al., 2001; Siebenaler and Caldwell, 1956). In those situations, helping behaviour is directed towards an individual in trouble. Little is known however about the factors and mechanisms underlying such behaviours. The extent to which captive and wild dolphins display other-regarding preferences or helping behaviours towards conspecifics in a flexible way and in different contexts deserves further research. Despite the null results of this pilot study, this experimental paradigm still represents a powerful tool for this purpose due to both its simplicity and the ease of controlling motivational and cognitive factors. Moreover, it even allows us to assess reciprocal and cooperative behaviours and the influence of social learning across sessions. Therefore, further studies might find positive results using variations of this paradigm which include the right motivators and factors.

Compliance with ethical standards

All applicable international, national and institutional guidelines for the care and use of animals were followed.

Declarations of interest

None.

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References

Albiach-Serrano, A., 2015. Cooperation in primates. A critical, methodological review. Interact. Stud. 16, 361–382. https://doi.org/10.1075/is.16.3.02alb.

Amici, F., Visalberghi, E., Call, J., 2014. Lack of prosociality in great apes, capuchin monkeys and spider monkeys: convergent evidence from two different food distribution tasks. Proc. R. Soc. B Biol. Sci. 281https://doi.org/10.1098/rspb.2014.1699. 20141699–20141699.

Barnes, J.L., Hill, T., Langer, M., Martinez, M., Santos, L.R., 2008. Helping behaviour and regard for others in capuchin monkeys (Cebus apella). Biol. Lett. 4, 638–640. https://doi.org/10.1098/rsbl.2008.0410.

Batson, C., Powell, A., 2003. Altruism and prosocial behavior. Handb. Psychol.

Brosnan, S.F., Houser, D., Leimgruber, K., Xiao, E., Chen, T., de Waal, F.B.M., 2010. Competing demands of prosociality and equity in monkeys. Evol. Hum. Behav. 31, 279–288. https://doi.org/10.1016/j.evolhumbehav.2010.02.003.

Brownell, C.A., Iesue, S.S., Nichols, S.R., Svetlova, M., 2013. Mine or yours? Development of sharing in toddlers in relation to ownership understanding. Child Dev. 84, 906–920. https://doi.org/10.1111/cdev.12009.

Burkart, J.M., van Schaik, C., 2013. Group service in macaques (Macaca fuscata), capuchins (Cebus apella) and marmosets (Callithrix jacchus): a comparative approach to identifying proactive prosocial motivations. J. Comp. Psychol. 127, 212–225. https://doi.org/10.1037/a0026392.

Burkart, J.M., Fehr, E., Efferson, C., van Schaik, C.P., 2007. Other-regarding preferences in a non-human primate: common marmosets provision food altruistically. Proc. Natl. Acad. Sci. U. S. A. 104, 19762–19766. https://doi.org/10.1073/pnas.0710310104.

Caldwell, M.C., Caldwell, D.K., 1966. Epimeletic (care-giving) behavior in Cetacea. In: Norris, K.S. (Ed.), Whales, Dolphins and Porpoises. University of California Press, Berkeley, pp. 755–789. https://doi.org/10.1017/CBO9781107415324.004.

Claidière, N., Whiten, A., Mareno, M.C., Messer, E.J.E., Brosnan, S.F., Hopper, L.M., Lambeth, S.P., Schapiro, S.J., McGuigan, N., 2015. Selective and contagious prosocial resource donation in capuchin monkeys, chimpanzees and humans. Sci. Rep. 5, 7631. https://doi.org/10.1038/srep07631.

Cockcroft, V.G., 1990. Observed and inferred epimeletic (nurturant) behaviour in bottlenose dolphins. Aquat. Mamm. 31–32.

Cronin, K.A., Schroeder, K.K.E., Rothwell, E.S., Silk, J.B., Snowdon, C.T., 2009. Cooperatively breeding cottontop tamarins (Saguinus oedipus) do not donate rewards to their long-term mates. J. Comp. Psychol. 123, 231–241. https://doi.org/10.1037/a0015094.

Dale, R., Despraz, M.-N., Marshall-Pescini, S., Range, F., 2019. Piloting a new prosociality paradigm in dogs and wolves: the location choice task. Behav. Processes 162, 79–85. https://doi.org/10.1016/j.beproc.2019.01.004.

de Waal, F.B.M., 2008. Putting the altruism back into altruism: the evolution of empathy. Annu. Rev. Psychol. 59, 279–300. https://doi.org/10.1146/annurev.psych.59.103006.093625.

de Waal, F.B.M., Leimgruber, K., Greenberg, A.R., 2008. Giving is self-rewarding for monkeys. Proc. Natl. Acad. Sci. U. S. A. 105, 13685–13689. https://doi.org/10.1073/pnas.0807060105.

Drayton, L., Santos, L., 2014. Insights into intraspecies variation in primate prosocial behavior: capuchins (Cebus apella) fail to show prosociality on a touchscreen task. Behav. Sci. (Basel) 4, 87–101. https://doi.org/10.3390/bs4020087.

Eskelinen, H.C., Winship, K.A., Jones, B.L., Ames, A.E.M., Kuczaj, S.A., 2016. Acoustic behavior associated with cooperative task success in bottlenose dolphins (Tursiops truncatus). Anim. Cognit. 19, 789–797. https://doi.org/10.1007/s10071-016-0978-1.

Greenberg, J.R., Hamann, K., Warneken, F., Tomasello, M., 2010. Chimpanzee helping in collaborative and noncollaborative contexts. Anim. Behav. 80, 873–880. https://doi.org/10.1016/j.anbehav.2010.08.008.

Herman, L.M., 2010. What laboratory research has told us about dolphin cognition. Int. J. Comp. Psychol. 23, 310–330.

Jaakkola, K., Guarino, E., Donegan, K., King, S.L., 2018. Bottlenose dolphins can understand their partner's role in a cooperative task. Dokl. Biol. Sci. 285https://doi.org/10.1098/rspb.2018.0948. 20180948.

Jensen, K., Hare, B., Call, J., Tomasello, M., 2006. What's in it for me? Self-regard precludes altruism and spite in chimpanzees. Proc. R. Soc. B Biol. Sci. 273, 1013–1021. https://doi.org/10.1098/rspb.2005.3417.

Kim, Y., Martinez, L., Choe, J.C., Lee, D.-J., Tomonaga, M., 2015. Orangutans (Pongo spp.) do not spontaneously share benefits with familiar conspecifics in a choice paradigm. Primates 56, 193–200. https://doi.org/10.1007/s10329-015-0460-8.

King, S.L., Allen, S.J., Connor, R.C., Jaakkola, K., 2016. Cooperation or dolphin 'tug-of-war'? Comment on Kuczaj et al. And Eskelinen et al. Anim. Cognit. 19, 1227–1229. https://doi.org/10.1007/s10071-016-1026-x.

Kuczaj, S., Tranel, K., Trone, M., Hill, H., 2001. Are animals capable of deception or empathy? Implications for animal consciousness and animal welfare. Anim. Welf. 10, 161–173.

Kuczaj, S.A., Winship, K.A., Eskelinen, H.C., 2015. Can bottlenose dolphins (Tursiops truncatus) cooperate when solving a novel task? Anim. Cognit. 18, 543–550. https://doi.org/10.1007/s10071-014-0822-4.

Lakshminarayanan, V.R., Santos, L.R., 2008. Capuchin monkeys are sensitive to others' welfare. Curr. Biol. 18, 999–1000. https://doi.org/10.1016/j.cub.2008.08.057.

Marino, L., Frohoff, T., 2011. Towards a new paradigm of non-captive research on cetacean cognition. PLoS One 6, e24121. https://doi.org/10.1371/journal.pone.0024121.

Melis, A.P., 2017. The evolutionary roots of prosociality: the case of instrumental helping. Curr. Opin. Psychol. https://doi.org/10.1016/j.copsyc.2017.08.019.

Melis, A.P., Warneken, F., Jensen, K., Schneider, A.C., Call, J., Tomasello, M., 2011. Chimpanzees help conspecifics obtain food and non-food items. Proc. R. Soc. B Biol. Sci. 278, 1405–1413. https://doi.org/10.1098/rspb.2010.1735.

Nakahara, F., Komaba, M., Sato, R., Ikeda, H., Komaba, K., Kawakubo, A., 2017. Spontaneous prosocial choice by captive bottlenose dolphins, Tursiops truncatus. Behav. Processes 135, 8–11. https://doi.org/10.1016/j.beproc.2016.11.009.

Pack, A.A., Herman, L.M., 2006. Dolphin social cognition and joint attention: our current understanding. Aquat. Mamm. 32, 443–460. https://doi.org/10.1578/AM.32.4.2006.443.

Preston, S.D., de Waal, F.B.M., 2002. Empathy: its ultimate and proximate bases. Behav. Brain Sci. 25, 1–20. https://doi.org/10.1017/S0140525X02000018.

Siebenaler, J.B., Caldwell, D.K., 1956. Cooperation among adult dolphins. J. Mammal. 37, 126–128. https://doi.org/10.2307/1375558.

Silk, J.B., Brosnan, S.F., Vonk, J., Henrich, J., Povinelli, D.J., Richardson, A.S., Lambeth, S.P., Mascaro, J., Schapiro, S.J., 2005. Chimpanzees are indifferent to the welfare of unrelated group members. Nature 437, 1357–1359. https://doi.org/10.1038/nature04243.

Skerry, A.E., Sheskin, M., Santos, L.R., 2011. Capuchin monkeys are not prosocial in an instrumental helping task. Anim. Cognit. 14, 647–654. https://doi.org/10.1007/s10071-011-0399-0.

Stevens, J.R., 2010. Donor payoffs and other-regarding preferences in cotton-top tamarins (Saguinus oedipus). Anim. Cognit. 13, 663–670. https://doi.org/10.1007/s10071-010-0309-x.

Takimoto, A., Kuroshima, H., Fujita, K., 2010. Capuchin monkeys (Cebus apella) are sensitive to others' reward: an experimental analysis of food-choice for conspecifics. Anim. Cognit. 13, 249–261. https://doi.org/10.1007/s10071-009-0262-8.

Tan, J., Hare, B., 2013. Bonobos share with strangers. PLoS One 8, e51922. https://doi.org/10.1371/journal.pone.0051922.

Vale, G.L., Davis, S.J., Lambeth, S.P., Schapiro, S.J., Whiten, A., 2017. Acquisition of a socially learned tool use sequence in chimpanzees: implications for cumulative culture. Evol. Hum. Behav. 38, 635–644. https://doi.org/10.1016/J.EVOLHUMBEHAV.2017.04.007.

Vonk, J., Brosnan, S.F., Silk, J.B., Henrich, J., Richardson, A.S., Lambeth, S.P., Schapiro, S.J., Povinelli, D.J., 2008. Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. Anim. Behav. 75, 1757–1770. https://doi.org/10.1016/j.anbehav.2007.09.036.

Warneken, F., Tomasello, M., 2006. Altruistic helping in human infants and young chimpanzees. Science (80-.) 311, 1301–1303. https://doi.org/10.1126/science.1121448.

Warneken, F., Hare, B., Melis, A.P., Hanus, D., Tomasello, M., 2007. Spontaneous altruism by chimpanzees and young children. PLoS Biol. 5, e184. https://doi.org/10.1371/journal.pbio.0050184.

Xitco, M.J., Gory, J.D., Kuczaj, S.A., 2001. Spontaneous pointing by bottlenose dolphins (Tursiops truncatus). Anim. Cognit. 4, 115–123. https://doi.org/10.1007/s100710100107.

Xitco, M.J., Gory, J.D., Kuczaj, S.A., 2004. Dolphin pointing is linked to the attentional behavior of a receiver. Anim. Cognit. 7, 231–238. https://doi.org/10.1007/s10071-004-0217-z.

Yamamoto, S., 2017. Primate empathy: three factors and their combinations for empathy-related phenomena. Wiley Interdiscip. Rev. Cognit. Sci. 8, e1431. https://doi.org/10.1002/wcs.1431.

Yamamoto, S., Tanaka, M., 2010. The influence of kin relationship and reciprocal context on chimpanzees' other-regarding preferences. Anim. Behav. 79, 595–602. https://doi.org/10.1016/j.anbehav.2009.11.034.

Yamamoto, S., Humle, T., Tanaka, M., 2009. Chimpanzees help each other upon request. PLoS One 4, e7416. https://doi.org/10.1371/journal.pone.0007416.

Yamamoto, S., Humle, T., Tanaka, M., 2012. Chimpanzees' flexible targeted helping based on an understanding of conspecifics' goals. Proc. Natl. Acad. Sci. 109, 3588–3592. https://doi.org/10.1073/pnas.1108517109.